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# The Neural Superposition Eye and Its Optical Demands

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*Summary.* A formal derivation of the optical demands of the neural superposition eye is presented. The treatment is based on a lattice description of the visual system using a H(orizontal) and V(ertical) axis.

Hence a relation for the interommatidial angles along these axes can be derived and the close connection between eye shape and facetlens pattern emerges. Possible general consequences for insect visual systems are discussed.

## A. Introduction

During the last decennium the eye of the fly has become a central theme in the study of the visual system of insects. Both anatomical and optical investigations have converged into the neural superposition theory of fly vision (for reviews see Kirschfeld, 1971; Trujillo-Cenóz, 1972; Braitenberg and Strausfeld, 1973). The optical requirements accordingly put to the structure of the eye of the fly are the topic of this paper.

In the struggle for the derivation of the ultimate relations it proved to be useful to treat the visual system of the fly as a set of two-dimensional lattices. As a corollary of the lattice approach we developed an index notation scheme, of which some applications have been described elsewhere (Stavenga, 1975; Stavenga and Beersma, 1975). Here we will restrict ourselves to the lattice structure of the neural superposition eye.

## B. Lattices

The pattern of the facetlenses in the cornea of a number of insect species has been discussed by Braitenberg (1967, 1970) and Trujillo-Cenóz (1972). In the housefly the facetlens pattern varies over the surface of the eye. Fig. 1 (modified from Braitenberg, 1970) diagrammatically shows a part of the left eye as viewed from the outside (see also Trujillo-Cenóz, 1972). In order to emphasize the lattice structure we have drawn horizontal and vertical lines through the facets, so defining a  $H$ - $V$  coordinate system.

The facetlenses can be regarded as points of a lattice (Kittel, 1968), drawn in Fig. 2. We notice that the cross-section of a facetlens is a proximity or Wigner-Seitz (primitive) cell. Actually the shape of a Wigner-Seitz cell is determined by

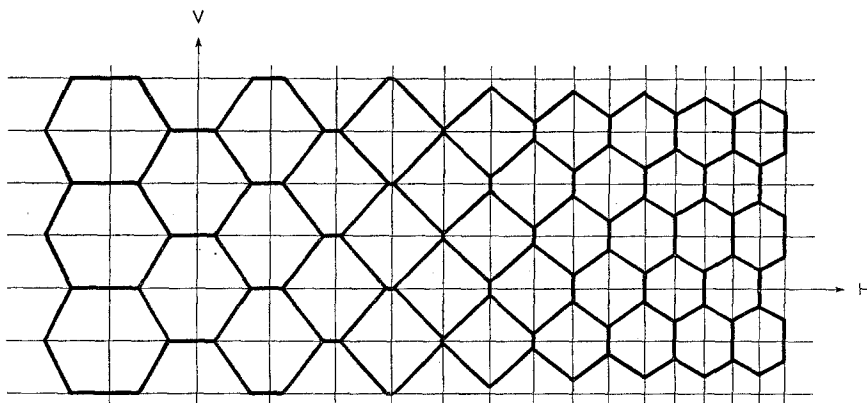


Fig. 1. Pattern of facellenses in the cornea of the left eye of a housefly (schematized). The  $H$ -axis points from anterior to posterior, the  $V$ -axis from ventral to dorsal. The two-dimensional lattice structure of the cornea is revealed by the horizontal and vertical lines

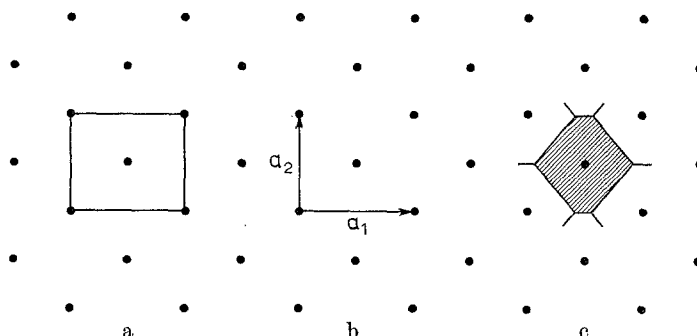


Fig. 2a—c. Part of a centered rectangular lattice. From left to right are shown: (a) the so-called unit-cell, which is a rectangle with a lattice point in its centre and a point on each corner; (b) the primitive translation vectors  $a_1$  and  $a_2$ ; (c) Wigner-Seitz or proximity cell which contains all points that are closer to the central lattice point than to any other lattice point; note the similarity to the cross-section of a facellens

the ratio  $a_2/a_1$  of the magnitudes of the primitive translation vectors  $a_1$  and  $a_2$  (Fig. 2)<sup>1</sup>.

A regular lens shape occurs (only) when  $a_2/a_1$  equals  $1/\sqrt{3}$ , 1 or  $\sqrt{3}$ . The three possible ideal lattices are (Fig. 3):

- a) lattice  $L_a$ , regular hexagons “lying” on the  $H$ -axis;
- b) lattice  $L_b$ , squares having diagonals parallel to the  $H$ - respectively the  $V$ -axis;
- c) Lattice  $L_c$ , regular hexagons “standing” on the  $H$ -axis.

The sets of open and closed circles in Fig. 3 represent the retinulae behind the facellenses. A retinula (Fig. 4) is the set of eight visual sense cells forming

<sup>1</sup> A Wigner-Seitz cell is obtained as follows: connect a given lattice point to all nearby lattice points; the lines normal to and bisecting these connecting lines enclose the Wigner-Seitz cell. It is also called a proximity cell because it contains all points that are closer to the central lattice point than to any other lattice point (cf. Kittel, 1968), see Fig. 2. The facellens pattern of Fig. 1 has been obtained by constructing the Wigner-Seitz cells in a centered rectangular lattice with constant  $a_2$  but with gradual decreasing  $a_1$ .

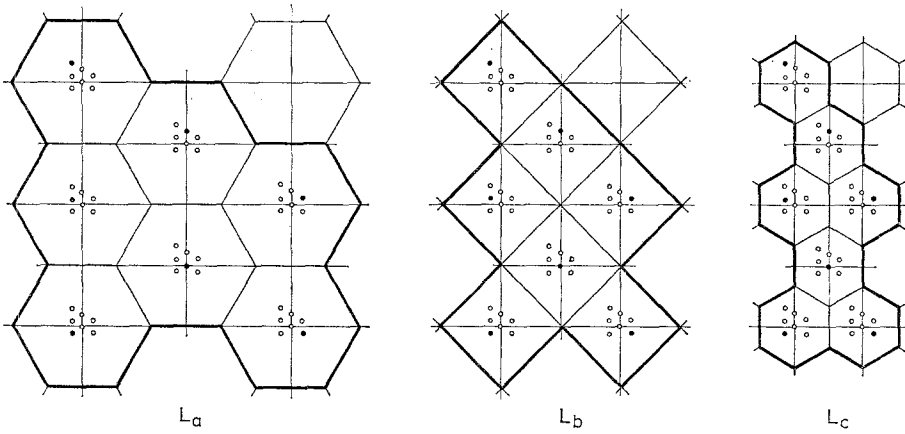


Fig. 3. The three possible regular facetlens patterns.  $L_a$ ,  $L_b$  and  $L_c$  occur at  $a_2/a_1$  equal to  $1/\sqrt{3}$ , 1 and  $\sqrt{3}$  respectively; see text

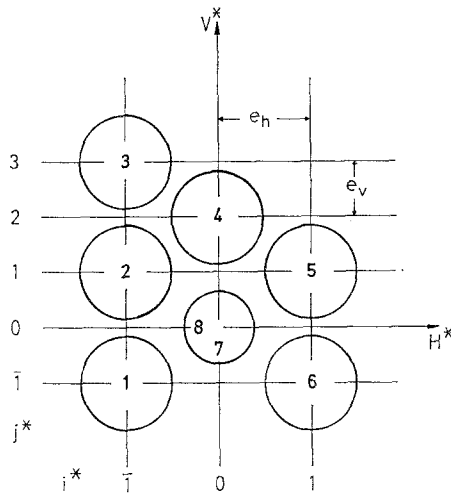


Fig. 4. Retinula lattice. The retinula sense cells  $R_1$  to  $R_8$  are represented by the rhabdomere pattern in the distal part of the retinula. Actually only the rhabdomere of  $R_7$  is present distally; the rhabdomere of  $R_8$  is located proximally, basal to that of  $R_7$ . Horizontal and vertical lines (interdistance  $e_v$  and  $e_h$  respectively) reveal that the retinula also can be considered as a part of a centered rectangular lattice. The relative  $H^*$ - and  $V^*$ -axes are parallel or antiparallel to the principal  $H$ - and  $V$ -axes, depending on the quadrant of the eye.

$i^*$  and  $j^*$  are relative indices (see Stavenga, 1975; Stavenga and Beersma, 1975)

part of one and the same ommatidium (cf. Braitenberg, 1970). Note that a retinula can also be regarded as a lattice of the centered rectangular type. According to the neural superposition theory of the eye of the fly the eight visual sense cells indicated in Fig. 3 by the closed circles have parallel visual axes, i.e. they look in the same direction (Kirschfeld, 1971; Trujillo-Cenóz, 1972; Braitenberg and Strausfeld, 1973). The corresponding optical demands will be derived below.

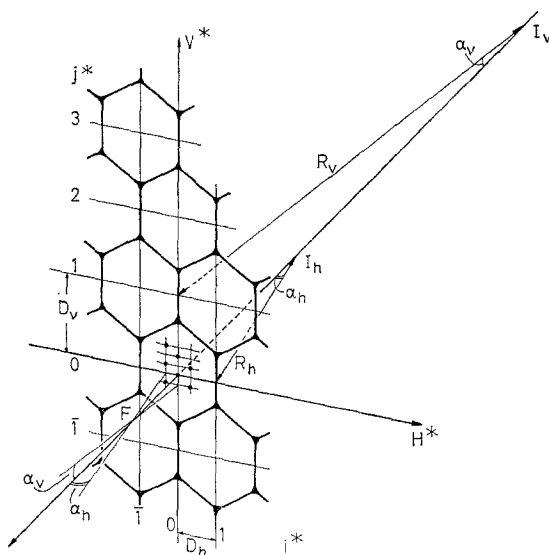


Fig. 5. Optics of the neural superposition eye. Shown is a set of seven ommatidia of which one of the peripheral retinula cells  $R_{1-6}$  of the peripheral ommatidia and the two central retinula cells  $R_{7,8}$  of the central ommatidium have parallel visual axes. Those cells were indicated in Fig. 3 with a black circle. Actually the facetlens pattern  $L_c$  (Fig. 3) has been redrawn together with the horizontal and vertical axes  $H^*$  and  $V^*$  and the facetlattice lines. The distance between these lines in the horizontal and vertical direction is  $D_h$  and  $D_v$  respectively.—In the facetlens of the central ommatidium the retinula lattice of Fig. 4 is depicted (cf. Fig. 3). This has been done for the sake of clarity; in fact, the retinula is localized proximally to the facetlens. But since the light receiving tips of the rhabdomeres coincide with the back focal plane, projection of the rhabdomere tips onto the facetlens is permitted if one considers only those light rays which share the focal point  $F$  of object space: all those rays are in image space propagated parallel to the (drawn) visual axis. The distance of  $F$  to the lens is the focal distance  $f$ .—Although the visual axis of the central ommatidium is given only, the other axes are easy to imagine. The visual axes of a vertical column of ommatidia determine a plane. These vertical planes intersect the central visual axis in  $I_h$ . The angle between the planes is  $\alpha_h = D_h/R_h$ , where  $R_h$  is the distance from  $I_h$  to the cornea. Similarly, horizontal rows of ommatidia determine planes which intersect the central visual axis in  $I_v$ . The angle between these planes is  $\alpha_v = D_v/R_v$ , where  $R_v$  represents the distance from  $I_v$  to cornea.—An analogous treatment can be given for the visual axes of the receptor cells located within one and the same ommatidium.—The neural superposition eye demands that  $\alpha_h$  is equal to the angle between adjacent vertical planes which are determined by the visual axes of cells arranged in vertical columns, and that  $\alpha_v$  equals the angle between horizontal planes (determined by the visual axes of horizontal rows of cells), or  $\alpha_h = e_h/f$  and  $\alpha_v = e_v/f$  (cf. Fig. 4).—Note that the distances to the lens of  $I_h$  and  $I_v$ , being  $R_h$  and  $R_v$  respectively, approximate the radii of curvature of the eye surface in horizontal and vertical directions

### C. The Optical Requirements of the Neural Superposition Eye

In order to derive the consequences of neural superposition for the optics of such an eye, we consider Fig. 5 showing a set of facetlenses together with the local vertical and horizontal lattice lines (cf. Fig. 1 and 3). The distance between these lines is  $D_h$  and  $D_v$  respectively. Now the visual axes of a column of ommatidia along the  $V^*$ -axis together determine an imaginary plane. (For definitions

of the relative  $H^*$ - and  $V^*$ -axes, see Stavenga, 1975.) The angle between those planes belonging to adjacent columns of ommatidia we call  $\alpha_h$ . Similarly the axes of rows of ommatidia along the  $H^*$ -axis determine planes between which the angle is  $\alpha_v$ . The points of intersection of these planes with the visual axis of the central ommatidium are  $I_h$  and  $I_v$  respectively (Fig. 5). The distance of these points to the cornea is called  $R_h$  and  $R_v$  respectively.

The visual axes of the columns and rows of photoreceptor cells within one retinula also define planes which enclose angles. If it may be assumed, following Kirschfeld and Franceschini (1968), that the light receiving site of the visual sense cells coincides with the focal plane of the facetlens these angles equal  $e_h/f$  and  $e_v/f$  respectively, where  $f$  is the focal distance, and  $e_h$  and  $e_v$  are the distances in the retinula lattice (Fig. 3).

Now the basic statement of the neural superposition theory is that the angle between the visual axes of neighbouring ommatidia equals the angle between the visual axes of corresponding photoreceptor cells within one retinula.

Hence the optical requirements for the neural superposition eye are represented by (see Figs. 4 and 5):

$$\alpha_h = \frac{D_h}{R_h} = \frac{e_h}{f} \quad (1)$$

$$\alpha_v = \frac{D_v}{R_v} = \frac{e_v}{f} \quad (2)$$

From these relations we derive

$$\frac{R_h}{R_v} = \frac{D_h}{D_v} \cdot \frac{e_h}{e_v} \quad (3)$$

and

$$\frac{\alpha_h}{\alpha_v} = \frac{e_h}{e_v}. \quad (4)$$

The ratio  $e_h/e_v$  determines the structure of the retinula lattice. Experimentally it appears that always  $e_h/e_v \simeq \sqrt{3}$  (cf. Boschek, 1971; Franceschini and Kirschfeld, 1971a; Beersma *et al.*, 1975). Furthermore, the ratio  $R_h/R_v$  indicates the shape of the eye and  $D_h/D_v$  characterizes the facetlens pattern.

Let us consider now the lattice types of Fig. 3. In the case of lattice  $L_a$  we have  $D_h/D_v = \sqrt{3}$ . Hence, from Eq. (3) it follows, with  $e_h/e_v = \sqrt{3}$ , that  $R_h = R_v$ . This means that the eye must have a spherical shape, if lattice type  $L_a$  exists. On the other hand,  $D_h/D_v = 1/\sqrt{3}$  holds in lattice  $L_c$ . Then Eq. (3) yields  $R_h = R_v/3$  (see Fig. 5). This outcome implies that in the case of the lattice  $L_c$  the local shape of the eye must be oval, the curvature in horizontal directions being three times stronger than the curvature of the eyes vertically. (Note that owing to the definition of  $R_h$  and  $R_v$  these quantities not necessarily equal exactly the radii of curvature.)

These results are revealing. It is well known that in the housefly and blowfly frontally the eye is about spherical and laterally the shape is quite oval, while the facetlens pattern gradually changes from  $L_a$  via  $L_b$  into  $L_c$ , going from posterior to anterior (Figs. 1 and 3; cf. Braitenberg, 1967, 1970; Trujillo-Cenóz, 1972). So it may be inferred that the changing facetlens pattern over the eye of flies keeps

pace with the varying local shape of the eye in order to fulfill the neural superposition principle.

Furthermore Eq. (4) means that the ratio of the angles  $\alpha_h$  and  $\alpha_v$  will equal (approximately) the value  $\sqrt{3}$  everywhere. Hence, although the facetlens pattern can show important variations, the arrangement of the visual axes essentially will be that of a hexagonal lattice (cf. Stavenga, 1975). The existence of this arrangement in the living blowfly has been proved in a brilliant way by Franceschini (1975).

The gained insight in the structure of the eye of the fly directly follows from the principle of neural superposition, by utilizing the fundamental equality of the lattices in the cornea (or retina) and the retinula.

#### D. Discussion

We have investigated the optics of the neural superposition eye by applying a coordinate system with two axes. Braitenberg (1970) on the other hand, treating the cornea lattices found in the *Drosophila* eye and that of the bee, i.e. the lattices  $L_a$  and  $L_c$  (Fig. 3), distinguishes three axes namely  $x$ ,  $y$ ,  $z$  and  $x$ ,  $y$ ,  $v$ , respectively;  $z$  conforms to our  $H$ -axis and  $v$  to the  $V$ -axis, while the  $x$ - and  $y$ -axes are parallel to oblique facet rows. Braitenberg (1970) criticizes Gemperlein (1969) who argues that two axes are sufficient to describe the pattern of facets of compound eyes, i.e. the  $d$ - and  $v$ -axes, which are identical to Braitenberg's  $x$ - and  $y$ -axes. Certainly Braitenberg is right in his criticism where he states that in Gemperlein's treatment the fundamental  $z(\equiv H)$ -axis fails. Nevertheless, two axes do suffice, since as we have shown above, the lattices  $L_a$  and  $L_c$  are special cases of a general type which is described satisfactorily with the  $H$ - and  $V$ -system.

Nice evidence for the fundamental value of the  $H$ - and  $V$ -axes can be distilled from optical investigations on the colours observable in the facetlenses of some diptera. Alternating bands of reddish and yellow-greenish facets in horsefly eyes emphasize the organization of the dipteran visual system in rows parallel to the  $H$ -axis (Bernard and Miller, 1968). Still more remarkable, in long-legged flies, facet rows as well as facet columns are coloured alternately either red or yellow. It will be noted that Trujillo-Cenóz and Bernard (1972), discussing the latter phenomena in relation with anatomical details of the retinulae, also use a  $H$ - $V$ -coordinate system (cf. Waterman and Horsch, 1966).

Basing ourselves on the two principal  $H$ - and  $V$ -axes we have been able to understand some essential features of the neural superposition eye, namely the relation between eye shape and facetlens pattern as well as the constant ratio  $\alpha_h/\alpha_v$  over the eye. Experimental investigations into the question of whether or not the optical requirements are met in the eyes of houseflies will be presented in the following paper (Beersma *et al.*, 1975).

Evidently our derivation applies to the eye of flies only, because only they have separate rhabdomeres. Most insects have a retinula with the rhabdomeres close together in a so-called fused rhabdom. It is striking to note, that in the bee, which possesses fused rhabdoms, the relation  $\alpha_h/\alpha_v \simeq \sqrt{3}$  nevertheless holds as well in the frontal eye region (Kirschfeld, 1973). By applying the reflection-pseudopupil method (Kirschfeld, 1965; Franceschini and Kirschfeld, 1971 b;

Franceschini, 1975) we observed also a  $\sqrt{3}$  ratio of the interommatidial angles in the ventral eye regions of the bee (unpublished measurements). Interestingly the facetlens pattern is approximately of the  $L_c$  type in all eye parts. Moreover the shape in all regions of the eye of bees is oval. So a similar relationship between facetlens pattern, eye shape and visual axes seems to exist not only in different regions of the housefly eye but also in the eye of other insects. We can speculate that, since the relation  $\alpha_h/\alpha_v = \sqrt{3}$  seems not to be a principal requirement of the visual system of bees, the actual hexagonal lattice structure of the visual axes may be realized in order to achieve a most efficient organization of the visual fields of neighbouring ommatidia for movement perception and/or pattern recognition.

We still remark that due to the retina and the higher order neural ganglia being homologous the lattice concept can be generalized to the entire visual system (cf. Stavenga and Beersma, 1975). For the present we conclude that the introduced lattice description has shown its usefulness in the study of the visual system of an important insect species.

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